Apical–basal polarity: why plant cells don't stand on their heads

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The anatomical terminology that is used to describe the orientation and polarity in the plant body (for distinction indicated here in italics) is based on the consensus agreement that the transition zone between the aerial and the soil-borne part (the root–shoot junction) is defined as the *base* of the plant, and the ends of a body axis – root and shoot tips – are defined as *apices* [1]. For embryos, another terminology is equally well established (indicated here by underlining), which defines the root embryo pole as the base and its opposite end as the apex [1]. Over the past few years, studies dealing with issues of cellular polarity in plants have used either anatomical or embryological terminology to describe the 'upper' and 'lower' side of individual cells. Recently, this confusion in terminology was highlighted, and it was proposed that the anatomical terminology should be used in all cases [2]. However, we believe that the anatomical terminology, when used for the description of cellular polarity, has important deficiencies. Here, based on a number of arguments, we propose what we consider to be a suitable compromise.

The anatomically well defined *base* of the plant is only vaguely defined functionally, and this becomes particularly apparent if one considers the transport of substances, for example, the strictly controlled unidirectional transport of the plant signalling molecule auxin [3]. All transported substances passing the anatomical *base* of the plant find their direction of movement suddenly changed from *basipetal* (towards the *base*) to *acropetal* (toward the *apex*) because the same transport stream is termed differently in shoots and roots. Physiologists have become used to this challenge, and it even proves to be an excellent selection criterion for distinguishing the bright but less attentive biology students from the more dutiful ones.

All adult plants originate from a single-celled zygote, whose pole of attachment to the maternal tissue is defined as basal and its opposite pole as apical [1]. This early polarity serves as a reference for a well-established term, the apical–basal body axis, and also for delineating the opposite poles of the embryo. Because it is not clear when and where the anatomical *base* of the embryo arises, all reports dealing with early development delineate the root pole (future position of the root *apex*) as the base of the embryo. It is an historical irony that the contrasting anatomical and embryological terminologies were coined in the same classical textbook on plant anatomy [1]. As long as their use is restricted to early embryo or post-embryonic development, respectively, their co-existence does not pose a major problem. However, recent reports indicate that the embryonic and post-embryonic establishment of growth axes share important features [4,5], providing a mechanistic reason against using two different terminologies. Note that for the post-embryonically initiated organs, such as lateral roots, flower organs or ovules, the proximal–distal convention is often used.

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Available online 13 December 2005

The anatomical and embryological terminologies have primarily been defined to describe the ends of larger structures such as organs, embryos and whole plants but not of individual cells. In recent studies dealing with problems of cell polarity, some biologists have chosen to use the anatomical terminology to delineate poles of individual cells, whereas others (including authors of this letter) refer to the zygote-derived main apical–basal axis, assuming that the cell polarity, as such, is conserved throughout the development [3–11]. When using the zygote-derived main apical–basal axis terminology, apical is the side of the cell facing the apical end of the ancestral zygote (in the adult plant facing the shoot *apex*) and basal is the opposite side (in the adult plant facing the root *apex*) regardless of the developmental stage and position of the cell. This contrasts with the anatomical terminology in the root, which describes the lower (basal) side of cells as *apical*. Positions of polarity markers, such as asymmetrically placed organelles or the asymmetrically localized PIN proteins, fit better with zygote-derived terminology. Thus, for example, PIN1 proteins positioned at the basal ends of provascular cells in the embryonic origin of the root meristem have not changed their position even though their localization in the same cells of the adult root meristem is named *apical*. In adult plants, they are localized at the same (lower) side of vasculature cells [3], regardless of whether this side is called *apical* (in the root) or *basal* (in the shoot). Even for post-embryonically initiated organs (aerial organs or lateral roots), the *de novo* established cell polarities seem to copy the situation along the main body axis, as demonstrated by the identical position of morphological and PIN polarity markers in developed organs [4]. In addition, studies into a regulator of apical–basal targeting of PIN proteins, PINOID [6], suggest that the underlying mechanisms of polar subcellular targeting are conserved throughout development. So, it does not seem that the establishment of cell polarity in plants uses an anatomical *base* as a biologically meaningful reference point.

The anatomical *apical–basal* terminology, unlike the zygotic polarity terms, cannot be used universally for the description of cell polarity because it necessitates continuous specification of the developmental stage and the position of the cell to know which cell side is meant. In addition, from the anatomical point of view, practical terms such as apical–basal-sorting, -targeting or -machinery that are regularly used in cell biology become obsolete because their meaning alternates depending on the position of the cell, whereas the underlying mechanisms do not. Because a rapid advance in our understanding of cellular polarity establishment in plants, as well as parallels to other systems, is to be expected, the disadvantages of anatomy-based terminology are likely to become more dramatic in the near future. Importantly, this would also make reports on cell polarity in plants less accessible to readers from other fields.

Anatomy-based *apical–basal* terminology is historically well established and suitable for describing the plant body and its parts [2]. However, for a description of the polarity of individual cells, the zygote-derived convention is more appropriate from a mechanistic, as well as from a practical, point of view. In the textbooks *Plant Hormones* [12] and *Polarity in Plants* [13], which were published recently, a balanced compromise for using the terms apical and basal was proposed and has been consistently used in many recent reports dealing with cellular polarity [3–11]. It suggests keeping the anatomical terms *apex*, *base*, *acropetal* and *basipetal* for postembryonic development but using the zygote-derived, apical–basal body axis as a reference for the description of the polarity of individual cells in cell biology. The root cells are the most problematic because the terms *apical* (anatomical) and basal (zygote-derived) describe the same (lower) cell side. To simplify things, for a plain description of cell sides within the root, one can use the intuitive and neutral terms upper and lower. However, when speaking about the underlying mechanism(s), apical–basal should be used. In early stages of organ primordia development, before the new polarities are clearly established, the proximal–distal convention can be used to avoid confusion (Figure 1). In the meantime, before a generally accepted consensus is reached, it should be unambiguously stated in each report which type of terminology is being used. Let us hope that the current terminology issue on polarity will not polarize the plant scientific community. It would be sad if such discussions distracted us from other – more scientifically relevant – issues.

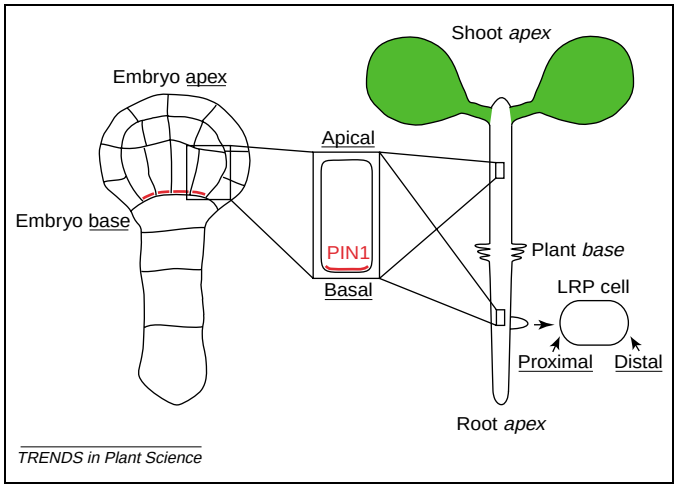

Figure 1. Apical–basal terminology in the plant embryo and seedling. For a description of the overall plant body, the anatomical terms such as shoot *apex* and root *apex* are maintained. For embryos, the zygote-derived terms are used. For a description of individual cells in any developmental context, the zygote-derived terminology is maintained. Thus, apical is always the upper side of cell (facing the shoot *apex*) and basal is the lower side (facing the root *apex*). This cellular terminology is supported by the uniform position of polarity markers such as PIN1 in embryo, shoot and root tissues. For cells or early organ primordia, such as lateral root primordia (LRP), without clearly defined cellular polarity, the proximal–distal convention is most appropriate.

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1360-1385/$ - see front matter
doi:10.1016/j.tplants.2005.11.010